ON THE RELATIONSHIP BETWEEN THE LENGTH OF THE POD AND FERTILITY AND FECUNDITY IN CERCIS

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(WITH ONE FIGURE)

It is well known to botanists that the egg cell is not the only structure affected by fertilization. GOEBEL points out[1] that in the Hepaticae an accompanying result is often seen in the production of a further development of the envelopes of the ripening sporangium. Again, in the same work he suggests[2] that the stimulus exercised by pollination in the flowering plants is most probably chemical. The preparation of the ovules for fertilization is dependent in some cases upon pollination. For instance, in such plants as *Corylus*, *Alnus*, *Quercus*, and some of their allies, there is no sign of the placenta in the ovary, to say nothing of ovules, at the time of pollination. In most species of Orchidaceae the ovules are laid down at the time of pollination, but still are rudimentary. The stimulus exercised by the pollen tube induces the further development of the female sexual apparatus in these plants.

PFEFFER[3] joins with GOEBEL in considering that the penetration of the pollen tube may serve as a stimulus to the development of the ovary, and cites the seedless fruits studied by MÜLLER-THURGAU and the observations on *Ficus* by TREUB.

JOST[4] writes: "The germination of the pollen tube has an exciting influence on the development of the fruit. This is particularly noticeable in certain cultivated plants, which, as for example currants and sultana raisins, produce no seeds, the ovules having degenerated. If the stigmas of these plants be not pollinated, the fruit fails to develop, but pollination leads to development without leading to any fertilization."

1 Organography of plants 2:105. 1902.

2 *Op. cit.* 1:269–270. 1900.

3 Physiology of plants (English transl.) 2:173. 1900–1906.

4 Lectures on plant physiology (English transl.) p. 370. 1907.

This is not the place for a review of the literature bearing upon these interesting chemical, physiological, and morphogenetic problems, however one wishes to designate them. The views of the three botanists just cited are sufficient to show the interest which is being taken in these problems. Several writers have contributed to the literature. Without any attempt at arrangement for priority or extent of investigation, I mention EWART (1, 2), SOLACOLU (7), TREUB (8), MÜLLER-THURGAU (5), NOLL (6), and FITTING (3). FITTING (4) has recently given a review, with a bibliography, of the chief literature in connection with an account of his own work on the Orchidaceae. From his experimental studies in this family he is led to the conclusion that the stimuli involved in the ontogeny of the fruit are in part due to an organic substance, not an enzyme, external to the pollen grain, in part to the growth of the pollen tubes, and finally in part to the development of the fertilized ovules.

The observations of the authors mentioned above deal chiefly with the influence of pollination as a stimulus inducing the development of the ovary up to a stage where the fertilization of the ovules is possible, or a little beyond. These phases of the problem are much more easily studied experimentally than that of the influence of the developing ovule upon the growth of the ovary. The present investigation bears upon this point.

If the developing seed excretes some substance which acts as a stimulus to the development of the ovary wall, or in some other manner exerts an influence upon it, it seems not unreasonable to suppose that the effect would be greater if several seeds were developing than if there were only one or a very few.

Our problem is essentially this: Does the number of ovules which develop to matured seeds influence the size of the fruit, and to what extent?

In all of the pods which have matured at least one seed, the stimulus to development due solely to the penetration of the pollen tube (as distinguished from the possible influence of the developing zygote) should be the same for all pods, unless the quantity of pollen tubes which penetrate the tissue of the style differs from ovary to ovary, and the intensity of the stimulus is to some extent proportional to their number. The problem is surrounded by a good many difficul-

ties. There seem to be at least four ways in which a relationship between the number of seeds developing and the size of the fruit might arise.

a. Fruits with a larger number of ovules are apt to be larger, if for no other reason, simply because the placental space required is greater. In the long run fruits with larger numbers of ovules also have larger numbers of seeds,[5] and an influence on fruit length at first attributed directly to the development of the seeds might be due indirectly to the number of ovules.

b. The space required for the matured seeds might, through the purely mechanical effects of crowding, result in the fruits with greater numbers of seeds being larger in size.

c. The developing seed might by means of some excreted product, or in some manner not yet suggested, directly induce a greater development of the ovary.

d. Both the number of ovules developing into seeds and the size attained by the fruit may be to some measure dependent upon some other character; say, for example, the position of the fruit on the inflorescence axis, or the number of fruits developing per inflorescence. The correlation between them might then be due merely to their mutual dependence upon some other character.

In the literature one finds only a few references to the relationship between the fertility of a fruit and its size. EWART (1) gives tables showing numbers of seeds and mean weight of fruit for three series of 125, 48, and 134 fruits of one variety of apples, which indicate that weight increases with number of seeds. According to EWART, MÜLLER-THURGAU found that in apples and pears the size of the fruit and the number of seeds are interdependent. MÜLLER-THURGAU cut off four of the five stigmas in the pear blossom, fertilized the remaining one, and thus produced asymmetrical fruit. EWART concludes: "Es steht demnach ohne zweifel fest, dass den Kern einen Wachtumsreiz auf die zur Fruchtbildung bestimmten Gewebe ausübt."

In view of the four possibilities suggested above, I think it is quite evident that great caution should be used in asserting that the number of ovules developing into seeds has *per se* any influence upon

[5] This statement is based on the results of many series of unpublished observations.

the size of the fruit. I believe that in such cases the analytical methods of modern higher statistics applied to large bodies of data are fitted to give results of real value.

The purpose of the present paper is to present the results of an attempt to measure the intensity of the interrelationship between the length of the pod and (*a*) the number of ovules formed, (*b*) the number of seeds developing, and (*c*) the fecundity, that is, the ratio of number of seeds developing to number of ovules formed per pod, in *Cercis canadensis*.

As material for a first study, the number of ovules formed and the number of seeds developing per pod were counted and the length measured in 3,000 pods, collected at Meramec Highlands, St. Louis, Missouri, in the autumn of 1905. To secure as representative material as possible, 50 pods from each of 60 individuals were taken. The measurements of pod length were taken to the nearest millimeter, and then grouped in classes of three millimeter range for purposes of calculation.

TABLE I

FERTILITY AND LENGTH OF POD FOR 3,000 *Cercis* FRUITS

	45–47	48–50	51–53	54–56	57–59	60–62	63–65	66–68	69–71	72–74	75–77	78–80	81–83	84–86	87–89	90–92	93–95	96–98	99–101	102–104	
$\frac{1}{2}$	..	..	..	1	..	..	...	...	...	...	...	...	...	...	..	..	..	..	..	..	1
$\frac{2}{2}$	..	..	1	2	1	7	4	4	1	...	...	...	...	1	..	..	..	..	..	..	21
$\frac{1}{3}$	2	1	1	3	3	2	...	1	...	...	...	...	...	...	..	..	..	..	..	..	13
$\frac{2}{3}$	1	1	1	3	6	8	9	8	3	5	2	1	1	...	..	..	..	..	..	..	49
$\frac{3}{3}$	..	..	1	1	8	10	20	24	27	18	14	4	1	1	..	..	..	..	..	..	129
$\frac{1}{4}$	..	..	..	..	1	1	2	...	...	...	...	...	...	...	..	..	..	..	..	..	4
$\frac{2}{4}$	..	..	..	3	9	14	22	16	12	11	7	4	2	1	..	..	..	..	..	..	101
$\frac{3}{4}$	..	..	2	11	9	37	72	62	56	57	57	24	8	4	..	..	..	..	..	..	399
$\frac{4}{4}$	1	..	..	2	4	23	48	78	• 94	102	99	60	40	13	5	...	..	..	..	..	569
$\frac{1}{5}$	..	..	..	..	..	...	1	...	...	...	...	...	...	...	..	..	..	..	..	..	1
$\frac{2}{5}$	..	..	1	..	1	5	2	1	2	1	1	2	2	1	..	..	..	..	..	..	19
$\frac{3}{5}$	..	..	1	2	3	14	18	21	20	16	22	10	7	2	..	1	..	1	..	..	138
$\frac{4}{5}$	..	..	1	1	3	13	22	54	67	70	74	48	33	19	3	8	1	2	1	..	420
$\frac{5}{5}$	..	..	..	..	2	5	17	30	58	115	115	96	59	48	20	11	..	..	1	..	577
$\frac{2}{6}$	..	..	..	1	..	...	...	...	...	1	...	1	...	...	..	..	..	..	..	..	3
$\frac{3}{6}$	..	..	..	..	..	1	3	3	2	4	2	2	...	...	..	..	..	..	1	..	18
$\frac{4}{6}$	..	..	..	..	1	2	7	4	10	22	16	10	6	2	1	2	..	..	..	..	83
$\frac{5}{6}$	..	..	..	..	..	4	3	6	16	23	36	39	29	16	5	6	..	1	..	1	185
$\frac{6}{6}$	..	..	..	..	..	..	4	3	19	22	38	45	38	25	10	7	4	3	4	2	224
$\frac{3}{7}$	..	..	..	..	..	...	...	...	...	...	...	1	...	...	..	..	..	..	..	..	1
$\frac{4}{7}$	..	..	..	..	..	..	...	..	...	...	...	...	...	...	..	..	..	..	..	..	0
$\frac{5}{7}$	..	..	..	..	..	1	...	...	1	1	1	3	1	...	..	..	..	..	..	..	8
$\frac{6}{7}$	..	..	..	..	..	...	1	...	1	1	3	2	2	3	2	2	..	..	..	..	17
$\frac{7}{7}$	..	..	..	..	..	...	...	...	2	5	...	5	3	1	1	2	1	..	..	..	20
	4	2	9	30	51	147	255	315	391	474	487	357	232	137	47	39	6	7	7	3	3000

Table I gives the data. In the first column to the left the number of ovules formed and the number of seeds developing per pod are

shown in the form of fractions, in which the number of ovules is given as the denominator and the number of seeds developing as the numerator. For each of the twenty-four seed-ovule classes found in our material, the frequencies of the different pod lengths are tabulated out.

The physical constants describing these characters are:

Average ovules	4.6947 ± 0.0111
Standard deviation of ovules	0.9041 ± 0.0079
Coefficient of variation of ovules	19.258
Average seeds	4.0613 ± 0.0134
Standard deviation of seeds	1.0849 ± 0.0094
Coefficient of variation of seeds	26.712
Average length of pod	76.181 ± 0.095
Standard deviation of length of pod[6]	7.6814 ± 0.0669
Coefficient of variation of length of pod	10.496
Average index, seeds/ovules	0.8650 ± 0.0020
Standard deviation of index	0.1587 ± 0.0014

These constants require no discussion here; they enable us to pass to the determination of the degree of interdependence of the fertility characters and the length of the fruit.

Consider first the correlation between number of ovules per pod and the length of the pod. We find $r_{ol} = 0.4278 \pm 0.0101$. Remembering that correlation is measured on a scale of 0 to ± 1, we see (*a*) that the sign of the relationship is positive, that is, that as the number of ovules per pod increases the length also increases, and (*b*) that the relationship is a moderately close one.

The degree of interdependence between the two characters may be made clearer by expressing it in terms of regression instead of correlation. The equation to the regression straight line is

$$y = 56.119 + 3.634x.$$

In this case y = length of pod and x = number of ovules per pod. From this equation we see that a pod having an ovule more than the average of the population would be 3.6 mm. longer than the average length.

[6] SHEPPARD'S correction was applied to the second moment in the calculation of the constants for length of pod. It was not used for the fertility characters, where we are dealing with integral variates, nor in the seed-ovule indices.

The regression line and the empirical mean length for the different numbers of ovules per pod are shown in a diagram (fig. 1). To the eye the agreement is very good, except at the upper extreme, where the observations are relatively few. We may obtain some idea of

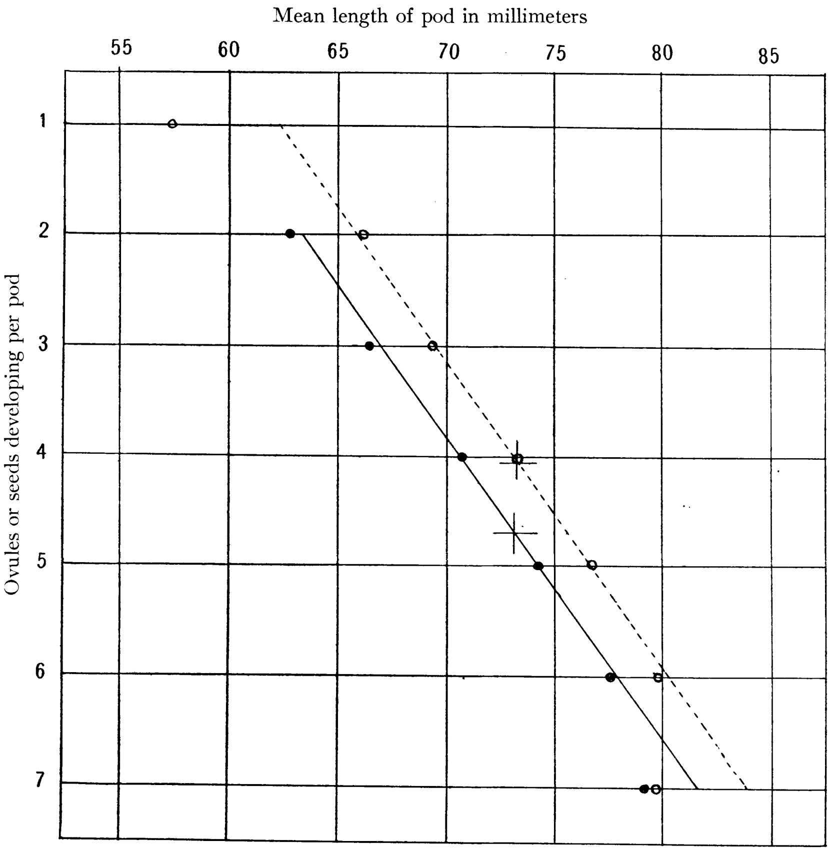

FIG. 1.—Diagram of slope of regression: straight lines, length on ovules and on seeds; solid line, theoretical length of pod for ovules; dotted line, theoretical length of pod for seeds; solid dots, observed length for ovules; circles, observed average length for seeds.

the amount of discrepancy between the theoretical line and empirical means by taking the average deviation on both sides of the line given by the equation. Considering the weight to be attached to a deviation to be proportional to the number of observations on which it is based,

we find average deviation $=0.248$ mm. A discrepancy of a fourth of a millimeter in a character such as the pod length of *Cercis* may seem to most biologists quite negligible, but I rather suspect that the falling off in mean pod length in pods with seven ovules is significant. The point is of little practical importance for our present discussion.

For number of seeds maturing per pod and length of pod we find the interdependence $r_{sl}=0.5055\pm0.0092$, and the equation to the regression straight line

$$y=58.645+3.579x,$$

where the significance of y is as above, and x = seeds per pod. The diagram (fig. 1) shows the agreement between the line given by the equation and the empirical means. Throughout the central region of the distribution of the number of seeds developing, the fit is very good, but at both ends the observed means fall considerably below those to be expected from the equation. If these deviations are biologically significant, and not due merely to the small number of observations which fall at the extremes of the range, they indicate that both the pods developing only a single seed and those developing the maximum number of seeds are somewhat dwarfed in length as compared with the whole series of 3,000 pods. I am not yet ready to discuss the reasons for this condition.

Comparing the constant for ovules and length, and seeds and length, we find

For ovules and length, $r=0.4278\pm0.0101$
For seeds and length, $r=0.5055\pm0.0092$

Difference $=0.0777$

Since the correlation is actually, though only slightly, higher for seeds developing than it is for number of ovules formed, it would appear that the number of seeds developing must have some connection with the length of the pod independent of the interdependence for length and ovules.

As pointed out early in this paper, one of the difficulties in asserting that there is a real physiological relationship between the number of seeds developing and the size of the fruit arises from the fact that

the correlation between the number of ovules formed and the size of the fruit may be of such a magnitude that it is impossible to tell without relatively refined statistical analysis whether the influence apparently due directly to the seeds may not be referred to the ovules. In the present case, for instance, the correlation for number of seeds developing exceeds only very slightly that for number of ovules formed.

We may determine whether the number of seeds developing has *per se* any correlation with the length of the pod by the following simple process. We sort our material into classes according to the number of ovules per pod, and then into subgroups according to the number of seeds developing, and determine the mean pod length for each of these subgroups. If now the length of the pod and the number of seeds developing are in some measure interdependent, we should expect to find significantly different mean lengths for pods of the same number of ovules, but different numbers of matured seeds.

TABLE II

MEAN LENGTH OF PODS FOR DIFFERENT NUMBERS OF SEEDS PER POD IN THE FOUR CHIEF OVULE CLASSES

Number of seeds per pod	Number of ovules per pod			
	3	4	5	6
1......	55.46	61.75	64.00	.....
2......	64.24	66.94	68.73	69.00
3......	68.37	69.06	70.37	72.00
4......	.....	72.41	73.85	73.97
5......	.....	.....	76.39	77.72
6......	.....	.....	.....	79.76

Such an arrangement of the data is given in table II for the classes in which the number of observations is sufficiently large to give smooth results. Here the results are very clearly favorable to the hypothesis of a relationship between the number of seeds developing and the length of the pod, independent of the relationship for number of ovules, for the mean increases as the number of seeds increases when we work with constant numbers of ovules per pod.

The same problem may be approached in another manner, that has the advantage of giving a terse quantitative statement of the independent relationship between the number of seeds developing

and the length of the pod. The partial correlation coefficient gives the correlation between two characters, say seeds (s) and length (l) for constant values of a third character, number of ovules (o).

A necessary preliminary is to determine the correlation between number of ovules per pod and number of seeds developing per pod. We find $r_{os}=0.7297\pm0.0058$. Clearly with such a large value for the correlation between ovules and seeds we would expect some relationship between the number of seeds developing and the length of the pod, having no direct physiological significance whatever, but due merely to the fact that since number of ovules and number of seeds are closely correlated, and number of ovules and length of pod are correlated, number of seeds and length of pod *must also be correlated.* It is the influence of the ovules which we wish to remove by means of the partial correlation coefficient. The familiar formula is

$$\rho_{sl}=\frac{r_{sl}-r_{os}r_{ol}}{\sqrt{1-r_{os}^2}\sqrt{1-r_{ol}^2}},$$

which gives

$$\rho_{sl}=0.3128\pm0.0111.$$[7]

I think this is a rather significant result. It not only shows that there is a physiological or morphogenetic relationship between the number of seeds developing and the length of the fruit independent of the correlation for ovules and length, but tells us the intensity of the interdependence as well.

There is still another way in which the influence of the ovules may be, to some extent at least, cleared away. Instead of correlating between the actual number of seeds maturing per pod and the length of the pod, the correlation between the relative number of seeds developing per pod (that is, the ratio or index seeds/ovules per pod) and the length of the pod may be found: $r_{il}=0.2906\pm0.0113$. This constant indicates very clearly that there is a real interdependence of number of seeds developing and fruit length, which is independent of the correlation for number of ovules and length of fruit.

[7] The probable error of ρ_{sl} is from the formula $E\rho_{sl}=0.67449.1-\rho_{sl}/\sqrt{n}$. Mr. DAVID HERON, of University College, London, tells me that he has recently demonstrated the correctness of this formula and has the proof in press.

Comparing the two methods of obtaining the independent correlation between number of seeds and length we have:

Correlation of index and length	0.2906 ± 0.0113
Partial correlation coefficient	0.3128 ± 0.0111
Difference	0.0222

This difference is certainly of no practical importance.

Summary

1. In considering the influence of the number of seeds developing upon the dimensions attained by the fruit, the number of ovules formed cannot be disregarded, since a correlation attributed directly to the influence of the development of the seeds may be in part at least due to an interdependence between the number of ovules formed and the dimensions of the fruit. The influence of the number of ovules can be neglected only when the coefficient of correlation between number of ovules and size of fruit is demonstrated to be zero. This point is well illustrated by a series of 3,000 pods of *Cercis*, where the correlations for ovules and length is $r_{ol} = 0.428 \pm 0.010$; while the correlation for seeds per pod and length is only $r_{sl} = 0.506 \pm 0.009$.

2. Two methods for freeing the correlation between the number of seeds developing and the length of the fruit from the influence of the relationship between the number of ovules formed and the length of the pod are suggested; the first is the determination of the partial correlation coefficient, that is, the correlation between number of seeds and length for constant values of numbers of ovules per pod; the second is the determination of the correlation between the index $\frac{\text{Seeds developing per pod}}{\text{Ovules formed per pod}}$ and the length of the pod.

The results from the data in hand are in close agreement,

$$\rho_{sl} = 0.313 \pm 0.011$$
$$r_{il} = 0.291 \pm 0.011$$

$$\rho_{sl} - r_{il} = 0.022$$

and we conclude that of the gross correlation of about $\rho = 0.500$ for number of seeds and length of pod a considerable portion, say $\rho = 0.300$ roughly, is due to some morphogenetic or physiological relationship between the number of seeds developing and the length of the pod.

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